

Scaling body size fluctuations

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The size of an organism matters for its metabolic, growth, mortality, and other vital rates. Scale-free community size spectra (i.e., size distributions regardless of species) are routinely observed in natural ecosystems and are the product of intra- and interspecies regulation of the relative abundance of organisms of different sizes. Intra- and interspecies distributions of body sizes are thus major determinants of ecosystems' structure and function. We show experimentally that single-species mass distributions of unicellular eukaryotes covering different phyla exhibit both characteristic sizes and universal features over more than four orders of magnitude in mass. Remarkably, we find that the mean size of a species is sufficient to characterize its size distribution fully and that the latter has a universal form across all species. We show that an analytical physiological model accounts for the observed universality, which can be synthesized in a log-normal form for the intraspecies size distributions. We also propose how ecological and physiological processes should interact to produce scale-invariant community size spectra and discuss the implications of our results on allometric scaling laws involving body mass.

protist microcosms | allometry | finite size scaling | body mass | cell counter

Why should a continuous, gap-free spectrum of organismic sizes emerge from the ecological and evolutionary processes that shape their ecosystems? The origins and the implications of the absence of preferential body sizes, which is routinely observed across a variety of ecosystems regardless of broad differences in climatic and environmental conditions (1–5), have been attracting much interest from field and theoretical ecologists (6–13). Scale invariance, epitomized by power-law probability distributions (9, 12, 14–19), requires regularities of the component parts (the species' size distributions) making up the whole [the community size spectra (i.e., the probability distributions of size regardless of species)]. In particular, a necessary condition for scaling community size spectra is the lack of peaks that pinpoint frequent occurrences, and therefore excess abundance (and vice versa) within any given range of sizes. Such features are particularly interesting if robust to environmental fluctuations because their dynamic origin could lie in the self-organization of complex adaptive systems (6, 9, 15).

Body size distributions in natural ecosystems are strongly related to the life history of the organisms and to the dynamics of their living communities (18). Thereby, they modulate structure and function of the ecosystem at any scale. Size spectra, which display the relative abundance of organisms of different sizes within or across species, convey a synoptic and possibly taxon-independent image of ecological communities (1, 2, 20, 21). As such, they have long been attracting much interest in ecology because they hold important predictive power (e.g., fish stock projections from planktonic size spectra) (2, 5). Because examples and counterexamples of scaling spectra abound (2, 3, 5, 7, 21–24), it is an unsettled issue as to whether scaling size spectra represent some central tendency of statistically stationary states of natural ecosystems. For instance, the operational computation of mean phytoplankton size was shown to depend on the sample size typically (7) and scaling relationships were documented for interspecific plant biomass (20, 25, 26), whereas some terrestrial

ecosystems exhibit ubiquitous gaps in size and uneven relative abundances of organisms (1, 21).

Single species inhabiting communities, however, do exhibit a species-specific mean and variance of their sizes, as even common sense suggests. Thus, there naturally exists the mean size of a particular species, as usually implied by most, if not all, biological scaling laws (10, 27–31), wherein one typical mass subsumes a whole distribution of sizes. One thus wonders how evolutionary and ecological processes interact to modulate species' abundances, the range of sizes proper to each functional group, and the number of species existing within a given niche or range of sizes to concoct regular, taxon-independent, continuous size spectra. Moreover, one expects that the existence of a range of possible sizes for a species (and how such a range varies for different mean sizes) has to be taken into account when addressing scaling laws in biology (e.g., allometric scaling laws) (10, 11, 27–29, 32–39).

Here, we have precisely measured the intraspecies size distributions of 13 species of protists in isolation or in competition (40–42), covering a relatively broad set of field conditions (*Materials and Methods*). Examples of such distributions as functions of the linear size in standard environmental conditions are shown in Fig. 1. The corresponding transformed distributions as functions of volume span over four orders of magnitude and are shown in Fig. 2A. Let $p_k(m)$ denote the measured size spectrum of the k th species: Such a $p_k(m)$ measures the relative proportion of individuals of a given species k with mass belonging to $(m, m + dm)$, assuming a continuous distribution of sizes. We tested whether $p_k(m)$ exhibits a finite-size scaling form (22, 30, 36, 43, 44) obtained by the product of two terms, an algebraic power of size multiplied by a suitable scaling function F ; that is,

$$p_k(m) = \frac{1}{m^\Delta} F\left(\frac{m}{\langle m \rangle_k^\phi}\right), \quad [1]$$

where $\langle m \rangle_k$ is the mean mass of the k th species and $F(x)$, critically, is the same scaling function for all species (dimensional analysis and normalization conditions that F must satisfy are discussed in *SI Text*). Eq. 1 implies that the only species dependence of the size distribution occurs through the average mass $\langle m \rangle_k$ of species k . Note that the two exponents in Eq. 1, Δ and ϕ , are not independent. This follows from imposing $\int_{\mathcal{R}} dm m p_k(m) \propto \langle m \rangle_k$ (where \mathcal{R} is the suitable range of sizes); in fact, $\int_{\mathcal{R}} dm m p_k(m) = \int_{\mathcal{R}} dm m \frac{1}{m^\Delta} F\left(\frac{m}{\langle m \rangle_k^\phi}\right) \propto \langle m \rangle_k^{(2-\Delta)\phi}$ is proportional to $\langle m \rangle_k$ only if the two exponents satisfy $(2 - \Delta)\phi = 1$

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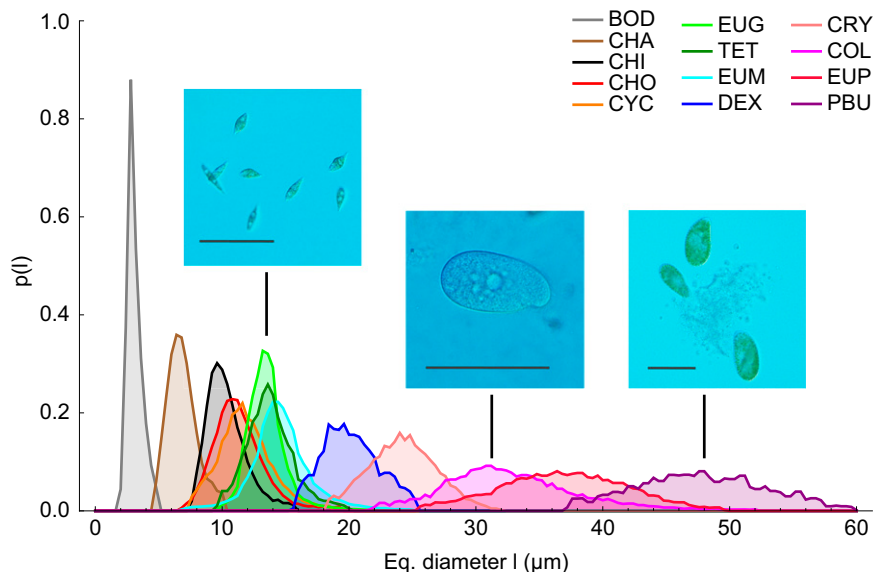


Fig. 1. Size distributions of 13 protist species as functions of the equivalent (Eq.) diameter (i.e., the diameter a cell would have if it were spherical). (Left to Right) Photographs show individuals of the species *E. gracilis*, *Colpidium* sp., and *P. bursaria*. (Scale bar: 100 μm .) The legend links each color to the corresponding species. (Protist photographs provided by Regula Illi, Eawag: Swiss Federal Institute of Aquatic Science and Technology, Dübendorf, Switzerland, and F.A.)

(details concerning constraints on the exponents are provided in *SI Text*). To verify the hypothesis, we plot $m^\Delta p_k(m)$ vs. $m/\langle m \rangle_k^\phi$ for all 13 protist species (Fig. 2B) and vary Δ and ϕ until a satisfactory data collapse (45) is observed. The best collapse is found for $\Delta = 1.0$ (and therefore $\phi = 1.0$; Fig. 2B). A quantitative method (46) to produce the best collapse yields $\Delta = 1.01 \pm 0.05$ (Fig. 2B, *Inset* and *SI Text*). A relevant consequence of Eq. 1, where $\Delta = \phi = 1$, is that the j th moment $\langle m^j \rangle_k = \int_0^\infty m^j p_k(m) dm$ is proportional to $\langle m \rangle_k^j$ (where $j = 1, 2, 3, \dots$). In particular, the variance of the species' sizes does increase with the mean size. The proportionality of successive moments ratios to $\langle m \rangle_k$ provides an independent test that further corroborates the validity of Eq. 1 (Fig. 2C and *SI Text*). We have thus found that a single parameter, the average mass of a species, is sufficient to characterize its size distribution fully. This is far from trivial because, in general, a probability distribution is determined by all its moments (47).

Environmental factors are capable of affecting the size distribution of any given species (48, 49). To test the effects of environmental conditions on Eq. 1, we question whether the measured size distributions might still be described by the universal functional form:

$$p(m) = \frac{1}{m} F\left(\frac{m}{\langle m \rangle}\right), \quad [2]$$

where $\langle m \rangle$ is the mean mass, critically determined (i) by the species or (ii) by phenotypic plasticity due to environmental factors. To that end, we have investigated a set of manipulated field conditions. Specifically, we grew some of the above protist species at different temperatures, or in pairwise competition with each other, over more than 15 generations to achieve relevant ecological time scales. Although obviously far from exhausting field-like scenarios, a sizeable plasticity was observed (Fig. 3A and *SI Text*). Crucially, once rescaled by the actual mean body size of the sample, whether constrained by temperature or by competition, all distributions collapse again and the scaling exponent estimate proves to be unaffected ($\Delta = 1.01 \pm 0.10$; Fig. 3B, *Inset*). Significantly, therefore, environmental factors are

capable of affecting the size distribution of any given species, although they do not alter its scaling nature because both the exponents and the scaling function F are unchanged.

The observed regularities are compelling, given the profound biological diversity of the species (belonging to the phyla/divisions of Ciliophora, Euglenozoa, Chlorophyta, and Cryptophyta) considered in this study (50). In addition, protists and unicellular algae are of key ecological significance. In fact, they are the basic food source of almost all aquatic food webs, and unicellular algae are responsible for almost 50% of the worldwide biomass production (51). Additionally, the observed universality of eukaryote intraspecies size distributions holds in a range of more than four orders of magnitude in mass. This suggests the existence of a simple underlying mechanism responsible for the empirical patterns observed. One possible explanation for the reported universality may be found in the physiological processes that determine the size of all unicellular species, namely, cellular growth and cell division. We found that a simple mathematical model of these processes (52–54) can justify the scaling form of unicellular eukaryotes' size distributions without the need to specify further biological details (*SI Text*). We therefore suggest that the universal features of intraspecies size distributions emerge from fundamental physiological constraints.

The detailed identification of the scaling function F in Eq. 2 is interesting but inessential for our tenet because the collapse of the distributions suffices in documenting the universality sought after. However, a log-normal functional form for $p(m)$ proves admissible and rooted in a theoretical framework for the time evolution of the distribution of body sizes in ecological time scales (Fig. 2D, *Inset* and *SI Text*). In this context, the size distribution of organisms of a given species is the stationary distribution of an Ornstein–Uhlenbeck process (55) in the variable $x = \log(m/\langle m \rangle)$ (56, 57). A log-normal form for $p(m)$ can also be recovered as a particular case of the physiological model cited above; thus, the two models are not mutually exclusive (*SI Text*).

A yet unproven but reasonable ansatz would posit that this behavior might apply to multicellular or arbitrarily complex organisms as well, resulting in even broader validity. An indication supporting this statement is the experimental size distribution of a multicellular organism that we measured with the same

a peak at small sizes exist due to debris in the culture (*SI Text*) (61). Peaks at larger sizes are due to protists. To deconvolve the two peaks, we fit the debris peak with an exponential decay (in a region adjacent to the peak, where data lie on a straight line in a log-linear plot; *SI Text*) and subtracted the resulting curve from the overall spectrum. On the right side of the protist peak, we truncated the data when the measured frequency of a size channel was below 20 occurrences to separate it from the noise. Noise was uniformly distributed on all size channels with a frequency of ~10–20 counts per channel, as demonstrated by measuring pure buffer solution only. For each species, several measurements of different cultures (grown in the same

conditions) were collected and summed to get an ensemble average representative of the species.

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Supporting Information

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SI Text

Meaning of Power Laws. Power laws are ubiquitous in nature. They have been shown to describe the similarity of the part and the whole of many objects in nature, ranging from coastlines, clouds, or mountain ranges (1) to natural or artificial networks like rivers (2) and up to complex social interactions (3–5). In general, a homogeneous power function [e.g., $f(x) = Cx^a$ with C, a constants] is intrinsically self-similar: If x is rescaled (multiplied by a constant), then $f(x)$ is still proportional to x^a , albeit with a different constant of proportionality. Such functions reproduce themselves on rescaling, and therefore lack natural scales, do not harbor a characteristic unit, and are said to be scale-free or true on all scales. Power-law probability distributions of size may imply an infinite mean, unless a finite range of sizes is assumed. In such a case and depending on the value of the scaling exponent, the mean, variance, and progressive moments of the distributions diverge in the infinite range. To be finite, they must depend on a finite interval of sizes sampled; thus, the mean makes no sense as a property of a population (6). This analog to the syndrome of infinite variance (1) (i.e., the progressive divergence of the variance of a self-similar or self-affine signal as the sample size is enlarged) is widely held as the typical signature of scale invariance.

Finite-Size Scaling Distributions. A general account of finite-size scaling (7) in ecology is provided by Banavar et al. (8). General properties of finite-size scaling distributions (as in Eq. 1) are detailed in a study by Banavar et al. (9) and its supplementary information. A brief account of the derivation of the most relevant results, adapted to the case at hand, is given in the following sections.

Normalization. Here, we study the normalization conditions for size distributions of the form:

$$p_k(m) = \frac{1}{m^\Delta} F\left(\frac{m}{\langle m \rangle_k^\phi}\right), \quad [\text{S1}]$$

where $\phi > 0$ and, for dimensional reasons:

$$F\left(\frac{m}{\langle m \rangle_k^\phi}\right) = \frac{1}{m_0^{1-\Delta}} \hat{F}\left(\frac{1}{m_0^{1-\phi}} \frac{m}{\langle m \rangle_k^\phi}\right), \quad [\text{S2}]$$

where m_0 is the minimum mass of an organism or a cutoff in the system. From this point onward, we will measure all masses in units of m_0 ; thus, F and \hat{F} coincide and $\frac{\langle m \rangle_k}{m_0} \rightarrow \langle m \rangle_k$ is arbitrarily large.

In order for the distribution in Eq. S1 to be normalized (i.e., $\int dm p_k(m) = 1$), one needs to make the following assumptions:

$F(x)$ approaches a constant when $x \ll 1$.

$F(x)$ goes to zero sufficiently fast when $x \gg 1$.

With these conditions, one has:

$$\begin{aligned} 1 &= \int_1^\infty dm p_k(m) = \int_1^\infty dm \frac{1}{m^\Delta} F\left(\frac{m}{\langle m \rangle_k^\phi}\right) = \\ &= \langle m \rangle_k^{\phi(1-\Delta)} \int_{\langle m \rangle_k^{-\phi}}^\infty dx \frac{1}{x^\Delta} F(x) = \\ &= \langle m \rangle_k^{(1-\Delta)\phi} \left[\int_{\langle m \rangle_k^{-\phi}}^1 dx x^{-\Delta} + \int_1^\infty dx x^{-\Delta} F(x) \right] = \\ &= a + b \langle m \rangle_k^{(1-\Delta)\phi}, \end{aligned} \quad [\text{S3}]$$

where a and b are constants. Now, except for corrections to the scaling [From Eq. S3: $p_k(m) = m^{-\Delta} F\left(\frac{m}{\langle m \rangle_k^\phi}\right) \left(a + b \langle m \rangle_k^{(1-\Delta)\phi}\right)^{-1} = m^{-\Delta} \left[\frac{1}{a} F\left(\frac{m}{\langle m \rangle_k^\phi}\right) - \frac{b}{a^2} \langle m \rangle_k^{(1-\Delta)\phi} F\left(\frac{m}{\langle m \rangle_k^\phi}\right) + \dots\right]$, which adds an additional term to Eq. S1], everything is consistent if $a = 1$, $(1 - \Delta)\phi < 0$, and $\Delta > 1$ ($\phi > 0$) or if $\Delta = 1$, in which case one has:

$$\begin{aligned} 1 &= \int_1^\infty dm p_k(m) = \int_1^\infty dm \frac{1}{m} F\left(\frac{m}{\langle m \rangle_k^\phi}\right) = \\ &= \int_{\langle m \rangle_k^{-\phi}}^\infty dx \frac{1}{x} F(x), \end{aligned} \quad [\text{S4}]$$

and two possibilities arise: (i) $\int_0^\infty dx \frac{F(x)}{x} = 1$, with $F(x) \rightarrow 0$ sufficiently fast for $x \rightarrow 0$ (which is consistent with our data), and (ii) $F(x) \sim_{x \rightarrow 0} (-\ln x)^{-\alpha}$, such that $\int_{\langle m \rangle_k}^\infty dx \frac{1}{x} F(x) \sim (\ln \langle m \rangle_k)^{\max(0, 1-\alpha)}$. If $\alpha > 1$, one is back to case i, whereas if $\alpha < 1$, one has logarithmic corrections to the scaling. In fact, if $\alpha < 1$, one finds $p_k(m) = \frac{1}{m} (\ln \langle m \rangle_k)^{1-\alpha} F\left(\frac{m}{\langle m \rangle_k^\phi}\right)$, (i.e., a logarithmic correction to the scaling).

Successive Moments Ratios. A test for the validity of a scaling size distribution of the form $p_k(m) = \frac{1}{m} F\left(\frac{m}{\langle m \rangle_k}\right)$ is the proportionality of successive moments ratios $\langle m^j \rangle_k / \langle m^{j-1} \rangle_k$ ($j > 1$) to the first moment $\langle m \rangle_k$. In fact, if $p_k(m) = \frac{1}{m} F\left(\frac{m}{\langle m \rangle_k}\right)$, one has:

$$\begin{aligned} \frac{\langle m^j \rangle_k}{\langle m^{j-1} \rangle_k} &= \frac{\int dm m^j \frac{1}{m} F\left(\frac{m}{\langle m \rangle_k}\right)}{\int dm m^{j-1} \frac{1}{m} F\left(\frac{m}{\langle m \rangle_k}\right)} = \\ &= \frac{\langle m \rangle_k^j \int dx x^j \frac{1}{x} F(x)}{\langle m \rangle_k^{j-1} \int dx x^{j-1} \frac{1}{x} F(x)} \propto \langle m \rangle_k, \end{aligned} \quad [\text{S5}]$$

where $x = \frac{m}{\langle m \rangle_k}$ and $j > 1$. In Fig. S1, we plot successive moments ratios calculated from our data [cultures in standard conditions (data are shown in Fig. 2; see also *Materials and Methods*)] and linear regressions on these data. The slopes of the linear regressions are compatible with the value of 1 (linear regressions

on log-transformed data). Coefficient of determination R^2 values for the regressions are $R^2_{(m^2)/(m)} = 0.999$, $R^2_{(m^3)/(m^2)} = 0.996$, and $R^2_{(m^4)/(m^3)} = 0.988$. The same is shown for the data of *Chilomonas* sp., *Euglena gracilis*, and *Euplotes aediculatus* in different environmental conditions in Fig. S2 (data are shown in Fig. 3; see also *Materials and Methods*). The slopes of the linear regressions are compatible with the value of 1 (linear regressions on log-transformed data). Coefficient of determination R^2 values for the regressions are $R^2_{(m^2)/(m)} = 0.998$, $R^2_{(m^3)/(m^2)} = 0.987$, and $R^2_{(m^4)/(m^3)} = 0.962$.

Modeling Cell Growth and Division. To model growth and cell division, we studied the scaling properties of a simple model for these two processes (10), focusing our attention on unicellular organisms of an unspecified single species. Here, we show that the model produces stationary size distributions as in Eq. 1.

Let $N(m, t)$ be the number of organisms of mass m at time t : A cell's mass grows exponentially in time with rate μ (i.e., $\dot{m} = \mu m$) and cell division occurs in time at a rate $b(m)$. Therefore, the fission rate depends on the mass of the cell [a mechanism known as sloppy size control (11)], and $b(m)dt$ is the probability that a cell of mass m divides in a time dt . We introduce a maximum possible size M for a cell [i.e., $N(m, t) = 0 \forall m > M$], which requires (10):

$$\int_0^M dm b(m) = \infty. \quad \text{[S6]}$$

Considering the balance of growth and division in an infinitesimal time interval dt and in the size interval $[m_1, m_2]$, expanding at first order in dt , one has:

$$\int_{m_1}^{m_2} dm \left(\frac{\partial N}{\partial t}(m, t) + \frac{\partial[\mu m N(m, t)]}{\partial m} + b(m)N(m, t) - 4b(2m)N(2m, t) \right) = 0. \quad \text{[S7]}$$

The equation governing the balance of growth and cell division is then:

$$\frac{\partial N}{\partial t}(m, t) + \frac{\partial[\mu m N(m, t)]}{\partial m} + b(m)N(m, t) - 4b(2m)N(2m, t) = 0. \quad \text{[S8]}$$

Let us assume that $N(m, t) = \lambda(m)e^{kt}$ at stationarity, where $\lambda(m)$ is proportional to the stationary cell size distribution. Introducing $N(m, t) = \lambda(m)e^{kt}$ in Eq. S8, one finds for $\lambda(m)$:

$$\mu \frac{d[m\lambda(m)]}{dm} = -[k + b(m)]\lambda(m) + 4b(2m)\lambda(2m). \quad \text{[S9]}$$

Integrating Eq. S9 in $[0, M]$, one then has the following:

$$k \int_0^M dm \lambda(m) + \mu \int_0^M dm \frac{d[m\lambda(m)]}{dm} = \int_0^M dm b(m)\lambda(m). \quad \text{[S10]}$$

Eq. S10 imposes $\int_0^M dm b(m)\lambda(m) < \infty$; therefore, in Eq. S6, one has $\lim_{m \rightarrow M} m\lambda(m) = 0$, which implies $\int_0^M dm \frac{d[m\lambda(m)]}{dm} = 0$, and as a result:

$$k = \frac{\int_0^M dm b(m)\lambda(m)}{\int_0^M dm \lambda(m)}. \quad \text{[S11]}$$

The scale invariance of $\lambda(m)$ can be deduced directly from Eq. S9 as follows. The value of λ depends on m and M [i.e., $\lambda = \lambda(m, M)$]. We assume that the total mass present at $t = 0$ is equal to 1 (Eq. S9 is linear in λ ; therefore, if λ is a solution, so is $C\lambda$ with C as an arbitrary constant). Because M is the only scale in the problem, we assume that $b(m, M) = \hat{b}\left(\frac{m}{M}\right)$ and rewrite Eq. S9 with $x = m/M$ as follows:

$$\mu \frac{d[x\lambda(Mx, M)]}{dx} = -[k + \hat{b}(x)]\lambda(Mx, M) + 4\hat{b}(2x)\lambda(2Mx, M), \quad \text{[S12]}$$

where $x \in [0, 1]$. Therefore, one has the solution $\lambda(Mx, M) = \hat{\lambda}(x)/M$ [i.e., $\lambda(m, M) = \frac{1}{M}\hat{\lambda}\left(\frac{m}{M}\right)$], which satisfies:

$$\mu \frac{d[x\hat{\lambda}(x)]}{dx} = -[k + \hat{b}(x)]\hat{\lambda}(x) + 4\hat{b}(2x)\hat{\lambda}(2x) \quad \text{[S13]}$$

in $x \in [0, 1]$, with $\int_0^1 dx \hat{\lambda}(x) = 1$ and $\hat{\lambda}(x) = 0 \forall x > 1$. In particular, the size distribution $p(m)$ can be written as:

$$p(m) = \frac{1}{mM} \hat{\lambda}\left(\frac{m}{M}\right) = \frac{1}{m} G\left(\frac{m}{M}\right). \quad \text{[S14]}$$

Computing the average mass $\langle m \rangle$, one finds that it is proportional to M :

$$\langle m \rangle = \int_0^M dm m p(m) = M \int_0^1 dy G(y) = cM, \quad \text{[S15]}$$

such that the stationary size distribution is of the form:

$$p(m) = \frac{1}{m} F\left(\frac{m}{m}\right), \quad \text{[S16]}$$

which is precisely the scaling ansatz proposed and observed in the data.

The solution to Eq. S13 can be written as $\lambda(x) = \lambda_n(x)$ with $2^{-n} \leq x \leq 2^{-n+1}$ for $n = 1, 2, \dots$ and

$$\lambda_n(x) = e^{-\int_{2^{-n}}^x dy h(y)} \left[C_n + \frac{4}{\mu} \int_{2^{-n+1}}^{2x} dy \frac{\hat{b}(y)}{y} \lambda_{n-1}(y) \right], \quad \text{[S17]}$$

where $\lambda_0(y) = 1$, $x \in [2^{-n}, 2^{-n+1}]$, $h(y) = [k + \hat{b}(y) + \mu]/y$, and C_0 depends on the normalization condition [i.e., $\int_0^1 dy \lambda(y) = 1$]. The C_n s ($n \geq 1$) are determined recursively imposing the continuity $\hat{\lambda}_n(2^{-n+1}) = \hat{\lambda}_{n-1}(2^{-n+1})$ for $n \geq 2$. For instance, if $n = 2$:

$$\hat{\lambda}_1(x) = C_0 e^{-\int_{1/2}^x dy h(y)} \Rightarrow \hat{\lambda}_1\left(\frac{1}{2}\right) = C_0 \quad \text{[S18]}$$

(note that $\hat{\lambda}_1(1) = 0$ due to the singularity in Eq. S6):

$$\hat{\lambda}_2(x) = e^{-\int_{1/2}^x dy h(y)} \left[C_1 + \frac{4}{\mu} C_0 \int_{1/2}^{2x} dy \frac{\hat{b}(y)}{y} e^{-\int_{1/2}^y dz h(z)} \right], \quad [\text{S19}]$$

and $\hat{\lambda}_2(1/2) = \hat{\lambda}_1(1/2) = C_0$ allows one to compute C_1/C_0 . Iterating, one can compute $C_n/C_0 \forall n \geq 1$.

Analytical Form of the Universal Size Distribution. A fitting procedure suggests the viability of an analytical log-normal form for the universal size distribution; that is,

$$p(m) = \frac{1}{m\sqrt{2\pi\sigma^2}} e^{-\frac{\left(\ln\left(\frac{m}{\langle m \rangle}\right) - \mu\right)^2}{2\sigma^2}}, \quad [\text{S20}]$$

where σ^2 and μ are constants, $\langle m \rangle$ depends on the species, and \ln is the natural logarithm (i.e., the logarithm to the base e). In order for the distribution in Eq. S20 to have the scaling form $p(m) = 1/mF(m/\langle m \rangle)$, one has to impose that $\langle m \rangle = \int_0^\infty dm mp(m)$, which implies $\mu = -\sigma^2/2$ (i.e., μ and σ are not independent). We thus propose the following analytical form for the universal size distribution, which depends on only one parameter, σ^2 :

$$p(m) = \frac{1}{m\sqrt{2\pi\sigma^2}} e^{-\frac{\left(\ln\left(\frac{m}{\langle m \rangle + \frac{\sigma^2}{2}}\right)\right)^2}{2\sigma^2}}. \quad [\text{S21}]$$

The scaling function $F(x)$ is therefore of the form:

$$F(x) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{\left(\ln\left(x + \frac{\sigma^2}{2}\right)\right)^2}{2\sigma^2}}, \quad [\text{S22}]$$

as suggested by the fact that a parabola fits the log-transformed data $mp(m)$ vs. $m/\langle m \rangle$ (least-squares fit on log-transformed data) well. To have a good estimate of the mean of F , we performed the fit to Eq. S22 in the common support of at least half of the protist species, with only one parameter, σ^2 . The best estimate for the parameter is $\sigma^2 = 0.222(3)$, and the coefficient of determination is $R^2 = 0.92$. The fit of the scaling function is shown in Fig. S3A, superimposed on the measured single-species size distributions. Fig. S3B compares the fit of a log-normal scaling function with the ensemble average of the experimental size distributions, showing a remarkable overlap.

We now turn to an illustration of how the postulated universal scaling form for $p(m)$ might arise from general dynamical considerations (9, 12, 13). Consider ecosystem dynamics over ecological time scales. Ecological processes governing the abundances and niche occupancy of species are expected to change their characteristic size. One would expect, however, that offspring would have a mass proportional to the mass of the parent organism (13). Thus, fluctuations in size within same species ought to be measured on the order of percent variations, and the natural variable is $x = \log(m/\bar{m})$ (12, 13), with \bar{m} being the characteristic mass of the reference species k (e.g., proportional to the mean $\bar{m} = \alpha(m)$) (9, 14). In this framework, the results of ecological processes can be represented by a random walk in the variable x , because a fixed percent increase (decrease) of the mass corresponds to a shift to the right (left) of the variable x by a constant amount. In the simplest model, the results of ecological processes could be represented by an Ornstein-Uhlenbeck process (15, 16). This process is a modification of a Wiener process, where the walk tends to move toward a central location, which, in the context of phenotypic evolution (12), has been identified as the optimum in the adaptive zone for the phenotype. A phenotypic character like body size, therefore,

is expected to be distributed around a fitness optimum in this framework. The physical analogy of this process is a noisy relaxation process (e.g., a spring fluctuating around its rest length in the presence of disturbances). The fraction of organisms $q(x, t)$ with a (log-)body mass x at time x is governed by the dynamical equation:

$$\frac{\partial q(x, t)}{\partial t} = D \frac{\partial^2 q(x, t)}{\partial x^2} + \frac{\partial [kxq(x, t)]}{\partial x}, \quad [\text{S23}]$$

where k is a constant, $k > 0$. The stationary solution is obtained by setting the rate of change of $q(x, t)$ to zero, and it is known to be Gaussian (15, 16):

$$q(x) = \sqrt{\frac{k}{\pi D}} e^{-\frac{kx^2}{2D}}. \quad [\text{S24}]$$

For the mass distribution, one then obtains $p(m)$:

$$p(m) = q(x) \frac{dx}{dm} = \frac{1}{m} \sqrt{\frac{k}{2\pi D}} e^{-\frac{k}{2D} \left(\ln\left(\frac{m}{\langle m \rangle}\right) - \ln \alpha\right)^2} \quad [\text{S25}]$$

(i.e., a log-normal distribution of mass). Imposing Eq. S25 to have mean $\langle m \rangle$, one finds $\alpha = \exp[-D/(2k)]$, and the distribution of size is therefore:

$$p(m) = q(x) \frac{dx}{dm} = \frac{1}{m} \sqrt{\frac{k}{2\pi D}} e^{-\frac{k}{2D} \left(\ln\left(\frac{m}{\langle m \rangle + \frac{D}{2k}}\right)\right)^2}, \quad [\text{S26}]$$

(i.e., a log-normal distribution of mass with mean $\langle m \rangle$ as in Eq. S21). Therefore, the scaling function F in Fig. 2 and Fig. S3 is $F(x) = \sqrt{\frac{k}{2\pi D}} \exp\left[-\frac{k}{2D} \left(\ln\left(x + \frac{D}{2k}\right)\right)^2\right]$.

One might wonder whether the size distribution obtained in Eq. S26 is in agreement with our model of cellular growth and division. The cellular growth and division model, as treated in the previous section, assumes the existence of a maximum mass M and allows one to study the scaling properties of the stationary size distribution. It is possible, however, to relax this hypothesis, allowing the cells to assume all masses in the range $[0, \infty]$ and to obtain an implicit relation for the stationary size distribution $p(m)$ (17), which allows one to compute the asymptotic behavior of the distribution for large mass (i.e., $m \rightarrow \infty$). In the notation of the previous section, the size distribution for large m satisfies the relation:

$$p(m) \rightarrow \frac{1}{m} \exp\left(-\int_{\alpha}^{m/\langle m \rangle} dy \frac{k+d(y)}{\mu y}\right), \quad [\text{S27}]$$

which behaves as a log-normal distribution if we further assume a division rate $d(y)$ increasing logarithmically with size [i.e., $d(y) \propto \ln y$].

On the Goodness of Data Collapses. Data collapse is a tool widely used in statistical physics to establish scaling laws and extract information on their exponents (18). Traditionally, the procedure to produce a data collapse is to rely on the direct visualization of it and on “eyeballing” the exponent that gives the best collapse. A less subjective method has been proposed (19), which introduces a measure (error functional E ; Figs. 2 and 3, *Insets*) to quantify the goodness of a collapse. Let Δ be the exponent that we tune to find the best collapse: $E(\Delta)$ is the cumulative area enclosed between all pairs of curves that we

try to collapse, within their common support, for the value Δ of the exponent. The value Δ^* of the exponent, which minimizes $E(\Delta)$, is taken as the best estimate for the exponent (i.e., the smaller the area, the better is the collapse). Errors are associated with the determination of Δ^* and are obtained from the width of the minimum. Further details can be found in the study by Bhattacharjee and Seno (19).

Community Size Spectra. In this section, we show how a power law community-size spectrum arises as a sum of single-species size distributions of finite-size scaling form (14). Assume that the size distribution of species k is of the form:

$$p_k(m) = \frac{1}{m} F\left(\frac{m}{(m)_k}\right). \quad [\text{S28}]$$

Let N_k be the stationary abundance of species k in an ecosystem [i.e., $N_k = N_k(t \rightarrow \infty)$] and S be the total number of species. The community size spectrum is defined as:

$$f(m) = \sum_{k=1}^S N_k p_k(m) / \sum_{k=1}^S N_k. \quad [\text{S29}]$$

We assume, supported by a number of observations (20), that the population abundance of the k th species scales as:

$$N_k \propto (m)_k^\alpha, \quad [\text{S30}]$$

where $\alpha < 0$ implies that the total number of organisms decreases with increasing typical size. From Eqs. S28 and S30, one has that:

$$f(m) \propto \sum_{k=1}^S N_k p_k(m) \propto \sum_{k=1}^S (m)_k^\alpha m^{-1} F\left(\frac{m}{(m)_k}\right). \quad [\text{S31}]$$

Let $g(\bar{m})$ be the fraction of species of typical size \bar{m} . The above equation can be rewritten, treating $(m)_k$ as a continuous variable for easiness of computation, as:

$$f(m) \propto \frac{1}{m} \int d\bar{m} g(\bar{m}) \bar{m}^\alpha F\left(\frac{m}{\bar{m}}\right) \propto \int dx g(xm) x^\alpha m^\alpha F\left(\frac{1}{x}\right). \quad [\text{S32}]$$

Theoretical predictions from a scaling macroecological framework (9, 14) and considerations on the total number of species on Earth (21, 22) suggest a pure power-law behavior for $g(\bar{m})$:

$$g(\bar{m}) \propto \frac{1}{\bar{m}^\beta}, \quad [\text{S33}]$$

which, because of normalization, is assumed to hold between an upper cutoff and a lower cutoff. One then has for the size spectrum $f(m)$:

$$f(m) \propto m^{\alpha-\beta} \int dx x^{\alpha-\beta} F\left(\frac{1}{x}\right) \propto m^{\alpha-\beta}, \quad [\text{S34}]$$

which has the form of a power law. Note, however, that the result still holds for log-normal species abundance distributions (22). In the case of a limited range of sizes, one might argue that the number of species S within the range of sizes investigated could be assumed as constant to first order. This, of course, is the particular case for which $\beta = 0$.

Overall, it is clear that to obtain a scaling community size spectrum (Eq. S29), a necessary condition is adaptive fine-tuning of the specific abundances. This is epitomized by the relation in Eq. S30, which, in turn, implies the thinning relations that are recurrent in the literature of macroecological empirical laws (9, 23).

Equal Biomass in Each Size Class. The case of $f(m) \propto m^{-2}$, which is routinely found in the literature (14, 24), is of special interest because it agrees with the assumption of constant biomass in each size class (25). In this case, the total mass in a range $(m, m + \Delta m)$ with $\Delta m/m \simeq 1$ is:

$$\int_m^{m+\Delta m} dx x f(x) \propto \log\left[1 + \frac{\Delta m}{m}\right] \simeq 1, \quad [\text{S35}]$$

such that the total biomass in a range between m and $m + \Delta m$, where Δm is the typical variance at scale m , is independent of m .

Bodo saltans Size Distribution. In Fig. 2, the size distribution of *Bodo saltans* (BOD) might seem not to collapse as well as that of the other species. This is due to an instrumentation limit and is not inherent to the BOD size distribution. BOD, in fact, has a mean volume of $17 \mu\text{m}^3$ and a mean equivalent diameter of $3.1 \mu\text{m}$. These values lie on the leftmost side of the size spectrum, where the debris peak is dominant and the instrument hardly resolves the peak of the protist culture (Fig. S4, *Inset*). As an effect of this, it is hard to separate the protist peak from the debris; consequently, the left side of the BOD size distribution is overestimated, causing a deviation from the other collapsing curves in Fig. 2. To show that this is indeed the case, we measured the size distribution of *Chlorogonium euchlorum* (CHO) with the 150- μm capillary of the Cell Counter and Analyzer System (CASY) model TTC (Roche Applied Science), whereas we used the 60- μm CASY capillary to obtain the data reported in the main text. Using the larger capillary, the protist and the debris peaks appear closer to each other (with there being fewer size channels in the [0, 20]- μm interval; Fig. S5, *Inset*), and as a result, the size of the CHO size distribution on the left is overestimated. If we plot the corresponding rescaled distribution, together with the other data of Fig. 2, we observe the same kind of deviation observed for BOD (Fig. S5). We argue, therefore, that if the instrumentation could resolve better the small-sized region of the BOD size distribution, it would collapse even better than it does in Fig. 2.

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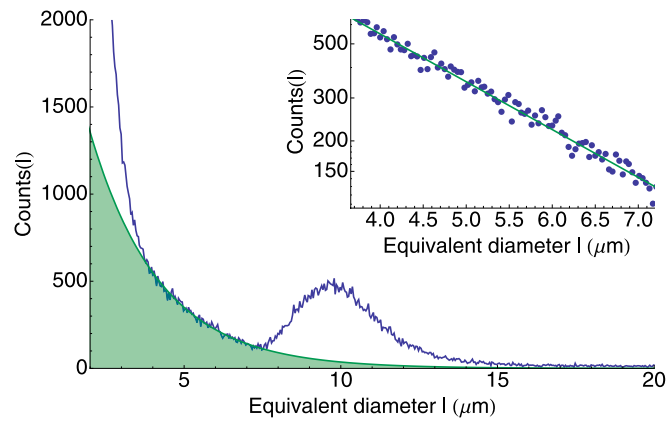


Fig. 56. Output of a measurement for *Chilomonas* sp. (CHI) culture. The superimposed exponential decay is the exponential fit of the debris in the region adjacent to the protist peak. (Inset) Decay of the debris to the left of the protist peak is exponential (straight line in a log-linear plot).

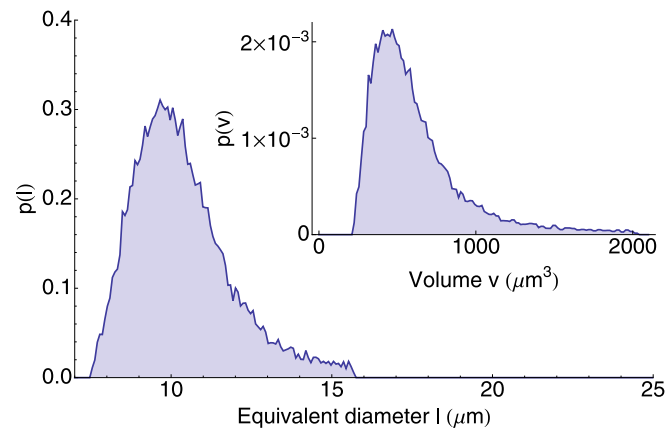


Fig. 57. Size distribution of *Chilomonas* sp. (CHI) as a function of the equivalent diameter. (Inset) Transformed volume size distribution of CHI.